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Pollen Morphology and Taxonomy of *Hedysarum* and Its Related Genera of the Tribe Hedysareae (Leguminosae–Papilionoideae)

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Pollen morphology of 51 species of the genera *Alhagi, Corethrodendron, Ebenus, Eversmannia, Hedysarum, Onobrychis, Stracheya* and *Taverniera* of the tribe Hedysareae was investigated. Three pollen types are recognized, i.e., tricolporoidate, tricolpate and tricolporate. The tricolporoidate type exhibits tricolporoidate apertures and perforate tectum, while the tricolpate or the tricolporate type are those with tricolpate or tricolporate apertures, respectively, with reticulate tectum. The tricolporoidate type is observed in *Alhagi, Corethrodendron, Eversmannia, Hedysarum* (section Membranacea of subgenus Gamotion and subgenus Heteroloma) and *Taverniera*. The tricolpate type is found in *Ebenus, Hedysarum* (sections Crinifera, Gamotion, Multicaulia and Subacaulia of subgenus Gamotion), *Onobrychis* and *Stracheya*, and is the most common in the tribe. The tricolporate type is found only in *Hedysarum* (subgenus Hedysarum). The tricolpate and tricolporate types are supposed to be derived from the tricolporoidate type, which is recognized here as most primitive in the tribe Hedysareae. Pollen morphological data of our study show that subgenus Hedysarum is separated from other infrageneric groups of *Hedysarum*, and that there is no substantial basis for separating *Corethrodendron, Stracheya* and *Taverniera* from *Hedysarum* as distinct genera. The former two are allied with the subgenus Heteroloma and the latter with the subgenus Gamotion.

Introduction

The tribe Hedysareae was created by Candolle (1825) and revised by Bentham (1865). Bentham's concept of the tribe was mostly adopted by Taubert (1894) and other subsequent taxonomists until a new circumscription was proposed by Hutchinson (1964) and Polhill (1981), although revised systems had been proposed by Gams (1923–24), Burkart (1939) and Schulze-Menz (1964), respectively. Taxonomic concepts and the historical changes of Hedysareae were reviewed by Ohashi (1971) under the name of Coronilleae.

Hutchinson (1964) accommodated nine genera in Hedysareae as *Alhagi, Corethrodendron, Ebenus, Eversmannia, Hedysarum, Onobrychis, Sartoria, Stracheya* and *Taverniera*. Polhill (1981), in the most recent circumscription of the tribe, recognized seven genera by revising Hutchinson's system excluding *Alhagi* from the tribe and merging *Corethrodendron* into *Hedysarum*. Discrepancies in recent treatments are the result of unsatisfactory circumscriptions of these genera due to a lack of evidence suggesting intergeneric relationships among them.

Hedysarum is the central genus of the tribe, but the system of the genus remains unrevised nearly a century since the most comprehensive monographic work

was made by Fedtschenko (1899, 1902). His system is, obviously, not satisfactory in nomenclature and in classification.

In order to contribute to the construction of a natural system of Hedysareae and *Hedysarum*, pollen morphology of the genera in the tribe is investigated. Pollen morphology has been shown to be one of the most important characters for the systematics of Hedysareae (Ohashi 1971, Ferguson and Skvarla 1981), but no detailed studies have been made, especially on the genus *Hedysarum*. Based on differences and similarities in pollen grains among the genera of the tribe and infrageneric taxa of *Hedysarum*, their relationships will be discussed in this paper.

Materials and Methods

Except for the monotypic genus *Sartoria* which is known in S. Turkey, representatives of all the genera of the tribe Hedysareae in the sense of Hutchinson (1964) and all the infrageneric groups of the genus *Hedysarum* were investigated under light and electron microscopes.

Pollen grains were obtained from herbarium specimens of the following herbaria: Natural History Museum, London, Great Britain (BM); Royal Botanic Garden, Edinburgh, Great Britain (E); Department of Botany, Faculty of Science, Kyoto University, Kyoto, Japan (KYO); Institute of Botany, Academia Sinica, Beijing, China (PE); Department of Botany, Faculty of Science, University of Tokyo, Tokyo, Japan (TI); Biological Institute, Faculty of Science, Tohoku University, Sendai, Japan (TUS). A list of taxa studied are given in Appendix I.

Observations were made on acetolysed pollen grains mounted in silicone oil under a Zeiss Photomicroscope-III equipped with the Nomarski differential interference contrast system (DIC). Acetolysis followed Erdtman's standard method (Erdtman 1960, 1966). Acetolysed pollen grains for scanning electron microscopy were dehydrated, critical point dried, coated with gold palladium, and examined with a JEOL JSM-840 scanning electron microscope (SEM). Polar and equatorial length were measured with SEM on 30 pollen grains of each individual. Acetolysed pollen grains for transmission electron microscopy were fixed in a 1% osmium tetroxide solution, dehydrated in an ethanol series, embedded in Spurr low viscosity epoxy resin and polymerized at 80°C for about 12 hours. Ultrathin sections of pollen walls were cut using an LKB Ultratome, and post-stained with uranyl acetate and lead citrate. The transmission electron micrographs were taken with a Hitachi H-500 microscope (TEM). Pollen terminology followed Erdtman (1966), Faegri and Iversen (1964) and Punt et al. (1994).

Results

Pollen morphology of the taxonomic groups of Hedysareae

Pollen grains were described in the following genera in the tribe Hedysareae: *Alhagi, Corethrodendron, Ebenus, Eversmannia, Onobrychis, Stracheya* and *Taverniera*. In *Hedysarum*, due to great diversity the pollen morphology is described separately for each infrageneric taxon. Pollen size is expressed by polar length × equatorial length in the following descriptions. The pollen features are summarized in table 1.

(1) **Alhagi** Adans. (Figs. 1–3)

Pollen grains 3-colporoidate, isopolar, prolate to subprolate, rounded in polar view, elliptic in equatorial view, 13.2–15.2 × 10.7–12.0 μm. Colpi long with blunt ends, with broad and smooth margins, sometimes constricted at the equator. Colpus membrane irregularly granular. Oroid formed by reducing the endexine along the polar axis, lolongate, about 4.0 μm long, the membrane corresponding to the endoaperture but often not persistent in acetolysed grains. Exine 0.4–0.6 μm thick. Sexine perforate to finely reticulate, much thicker than the nexine. Muri relatively

Table 1. Pollen features of the tribe Hedysareae

Taxon	Size (μm) (range and [mean])	Shape (P/E) (range and [mean])	Sexine	Aperture	Habit
Alhagi	13.2-[14.2]-15.2	1.12-[1.26]-1.36	perforate to finely reticulate	tricolporoidate	shrub
Eversmannia	15.0-[16.0]-17.2	1.31-[1.43]-1.56	perforate to finely reticulate	tricolporoidate	shrub
Taverniera	16.9-[17.8]-18.8	1.32-[1.42]-1.52	reticulate	tricolporoidate	shrub
Corethrodendron	15.0-[16.5]-17.7	1.39-[1.46]-1.59	reticulate	tricolporoidate	shrub
Hedysarum					
subg. Hedysarum	17.3-[19.8]-24.1	1.34-[1.69]-2.13	reticulate	tricolporate	annual or perennial
subg. Gamotion					
sect. Gamotion	17.0-[21.1]-25.8	1.36-[1.72]-2.23	reticulate	tricolpate	perennial
sect. Crinifera	16.3-[17.9]-19.3	1.60-[1.77]-1.88	reticulate	tricolpate	perennial
sect. Membranaceae	14.7-[16.2]-18.8	1.13-[1.25]-1.42	reticulate	tricolporoidate	suffrutescent
sect. Multicaulia	16.4-[19.4]-23.1	1.38-[1.77]-2.15	reticulate	tricolpate	perennial
sect. Subacaulia	17.7-[20.5]-25.8	1.36-[1.69]-2.04	reticulate	tricolpate	perennial
subg. Heteroloma	15.8-[17.3]-18.8	1.28-[1.54]-1.68	finely reticulate	tricolporoidate	shrub
Stracheya	23.6-[25.5]-27.8	1.48-[1.61]-1.79	reticulate	tricolpate	perennial
Ebenus	25.0-[26.2]-28.0	1.85-[2.05]-2.30	reticulate	tricolpate	perennial
Onobrychis	26.2-[28.4]-30.4	1.75-[2.09]-2.34	reticulate	tricolpate	perennial

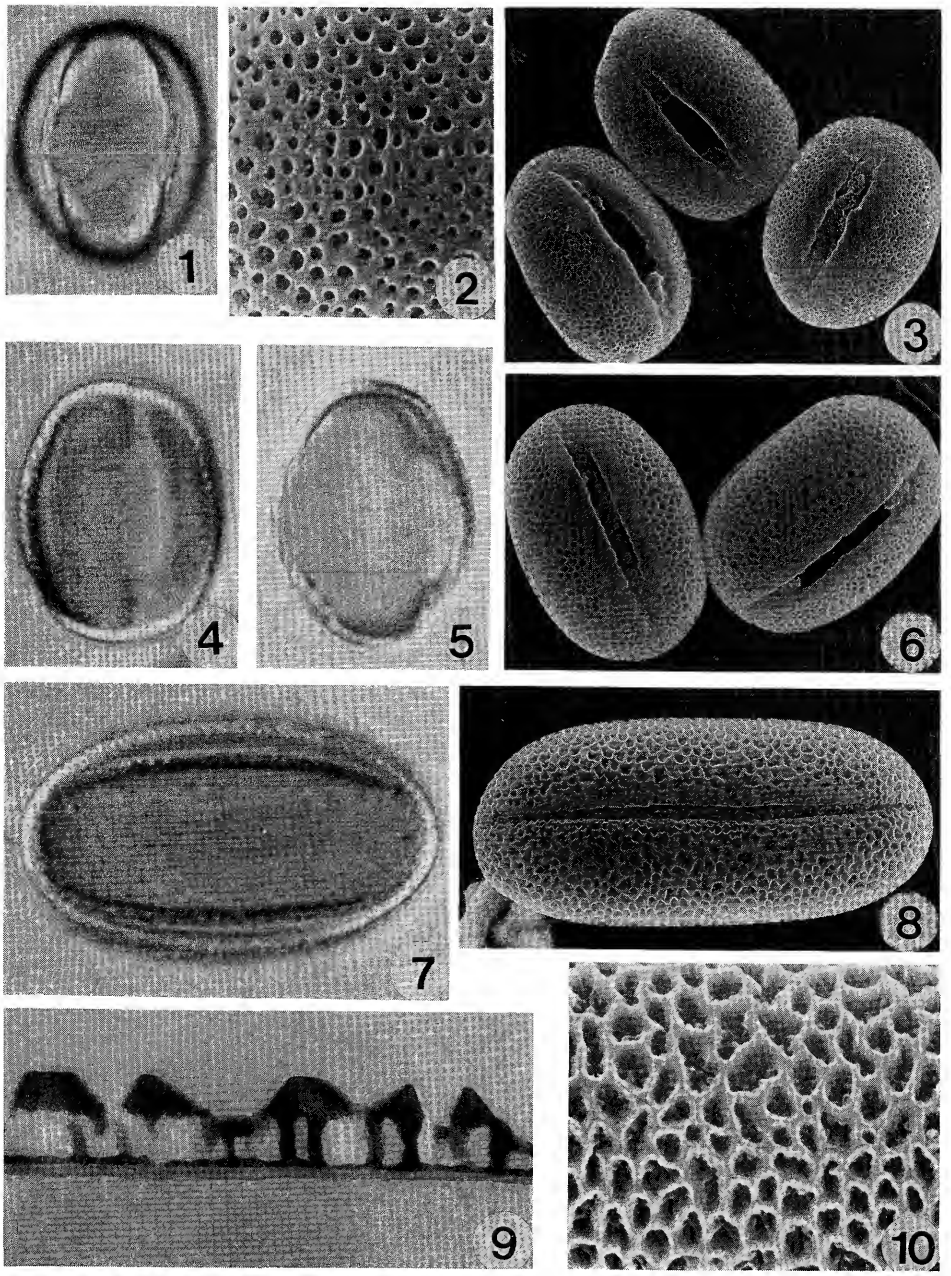
wide, keeled. Lumina rounded, diminishing in size towards the colpus margins and mesocolpium, occasionally with granules. Sporoderm stratification (EM): Tectum (0.15–0.21 μm thick), columellae (0.12–0.20 μm high), foot-layer (0.08–0.12 μm thick) and endexine (0.05–0.08 μm thick).

(2) **Corethrodendron** Fisch. & Basiner (Figs. 4–6)

Pollen grains 3-colporoidate, isopolar, prolate to subprolate, rounded in polar view, elliptic in equatorial view, 15.0–17.7 × 10.3–12.2 μm. Colpi long with acute ends, with broad and smooth margins. Colpus membrane irregularly granular. Oroid formed by reducing the endexine along the polar axis, relatively large, lolongate, about 7 μm long, the membrane corresponding to endoaperture often not persistent in acetolysed grains. Exine 0.5–0.7 μm thick. Sexine reticulate, about two times thicker than the nexine. Muri relatively wide, keeled. Lumina rounded, diminishing in size towards the colpus margins and mesocolpium. Sporoderm stratification (EM): Tectum (0.20–0.26 μm thick), columellae (0.18–0.21 μm high), foot-layer (0.04–0.08 μm thick) and endexine (0.06–0.15 μm thick).

(3) **Ebenus** L. (Figs. 7–10)

Pollen grains 3-colpate, isopolar, prolate to perprolate, rounded in polar view, compressed oval in equatorial view, 26.2–30.4 × 12.3–15.5 μm. Colpi long with acute ends, with narrow margins, the membrane finely granulated in one row. Exine 0.8–0.9 μm thick. Sexine evenly reticulate, much thicker than the nexine. Muri relatively wide, distally trapezoidal to keeled, proximally bumpy due to protruded columellae. Lumina rounded to ellipsoidal. Endexine increasing in thickness towards the colpus margins.



Figs. 1–10: Pollen grains of *Alhagi* (1–3), *Corethrodendron* (4–6) and *Ebenus* (7–10). Figs. 1–3: *Alhagi maurorum*. Fig. 1. Meriodional optical section of endexine showing long thinning endexine in equatorial region, with Nomarsky differential interference-contrast (DIC) microscope, LM × 2000. Fig. 2. Mesocolpium, perforate tectum, SEM × 8000. Fig. 3. Equatorial views showing ruptured area corresponding to endoaperture, SEM × 2000. Figs. 4–6: *Corethrodendron scoparium*. Fig. 4. Surface view showing lolongate endoaperture, LM × 2000. Fig. 5. Meriodional optical section of endexine showing long thinning endexine in equatorial region, LM with DIC × 2000. Fig. 6. Equatorial views showing ruptured area corresponding to endoaperture, SEM × 2000. Figs. 7–10: *Ebenus sibthorpii*. Fig. 7. Meriodional optical section of endexine showing continuous endexine on colpus margins, LM with DIC × 2000. Fig. 8. Equatorial view showing granulate colpus membranes in one row, SEM × 2150. Fig. 9. Cross section of mesocolpium showing exine stratification, TEM × 17000. Fig. 10. Mesocolpium, reticulate tectum, SEM × 7000.

Sporoderm stratification (EM): Tectum (0.34–0.38 μm thick), columellae (0.30–0.35 μm high), foot-layer (0.04–0.08 μm thick) and endexine (0.08–0.12 μm thick).

(4) **Eversmannia** Bunge (Figs. 11-16)

Pollen grains 3-colporoidate, isopolar, prolate to subprolate, rounded in polar view, elliptic in equatorial view, 15.0–17.2 × 10.8–12.2 μm. Colpi long with blunt ends, broad and smooth margins, sometimes constricted at the equator. Colpus membrane irregularly granular. Oroid formed by reducing the endexine along the polar axis, lolongate, about 4.3 μm long, the membrane corresponding to the endoaperture often not persistent in acetolysed grains. Exine 0.5–0.7 μm thick. Sexine perforate to finely reticulate, much more thicker than the nexine. Muri relatively wide, keeled. Lumina rounded, diminishing in size towards the colpus margins and mesocolpium. Sporoderm stratification (EM): Tectum (0.20–0.25 μm thick), columellae (0.15–0.30 μm high), foot-layer (0.06–0.12 μm thick) and endexine (0.04–0.10 μm thick).

(5) **Hedysarum** L.

The infrageneric system of the genus *Hedysarum* adopted in the present study principally follows that of Fedtschenko (1899, 1902), except the subgenus Gamotion. It is as follows:

(5-1) Subgen. Hedysarum

(5-2) Subgen. Gamotion (Basiner) B. Choi & H. Ohashi[1]. Lectotype: *H. alpinum* L.

(5-2-1) Sect. Gamotion Basiner. Lectotype: *H. alpinum* L.

(5-2-2) Sect. Crinifera (Boiss.) B. Fedtsch. Lectotype: *H. callithrix* Bunge.

(5-2-3) Sect. Membranacea B. Fedtsch. Lectotype: *H. membranaceum* Coss. & Bal.

(5-2-4) Sect. Multicaulia (Boiss.) B. Fedtsch. Lectotype: *H. formosum* Fisch. & Mey.

(5-2-5) Sect. Subacaulia (Boiss.) B. Fedtsch. Lectotype: *H. candidum* Bieb.

(5-3) Subgen. Heteroloma B. Fedtsch. Lectotype: *H. fruticosum* Pall.

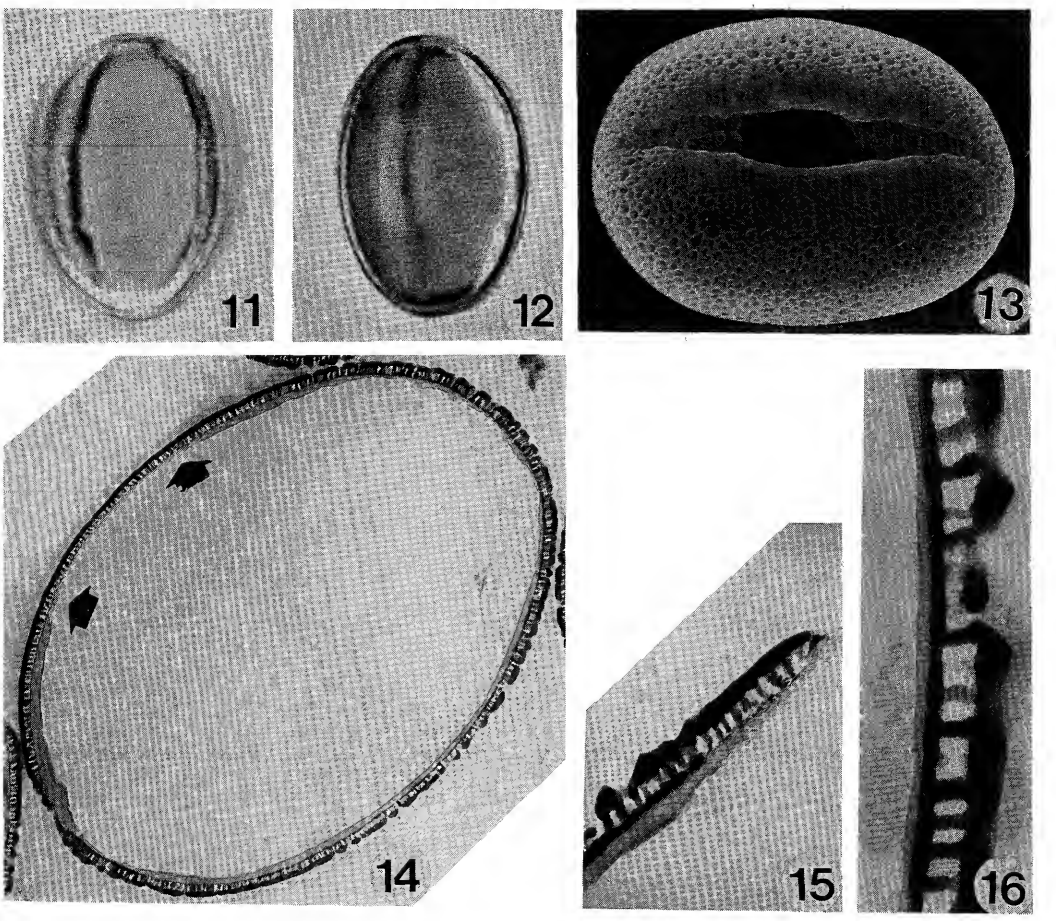
(5-1) Subgen. **Hedysarum** (Figs. 17–25)

Pollen grains 3-colporate, isopolar, prolate to less frequently perprolate, rounded in polar view, elliptic to compressed oval in equatorial view, 17.3–24.1 × 9.8–13.6 μm. Colpi long with acute ends, without margins. Colpus membrane finely to coarsely granular. Ora bordered by heavy thickenings (costae) on the polar axis and by weak thickenings on the equatorial axis of the endexine, relatively large, circular, 4–5 μm in diameter, with finely granulate membrane, the membrane often not persistent in acetolysed grains. Exine 0.5–0.6 μm thick. Sexine reticulate, much thicker than the nexine. Muri markedly keeled, proximally bumpy due to protruding columellae. Lumina polygonal, largest near the ora, decreasing in size towards the mesocolpium or apocolpium, sometimes with free projections. Sporoderm stratification (EM): Tectum (0.14–0.2 μm thick), columellae (0.17–0.30 μm high), foot-layer (0.05–0.08 μm thick) and endexine (0.04–0.08 μm thick).

(5-2) Subgen. **Gamotion** (Basiner) B. Choi & H. Ohashi

(5-2-1) Sect. **Gamotion** Basiner (Figs. 26–35)

Pollen grains 3-colpate, isopolar, prolate to perprolate, rounded in polar view, 17.0–26.5 × 10.2–14.5 μm. Colpi long with acute ends, almost reaching the poles, slightly marginate, membrane granulated in one row or operculate. Exine 0.6–0.8 μm thick, sexine about three times thicker than the nexine. Tectum reticulate, decreasing in size towards the mesocolpium and apocolpium, the apocolpium with a sculpture pattern similar to the mesocolpium. Muri relatively wide, distally trapezoidal to keeled, proximally bumpy due to protruding columellae. Lumina rounded to ellipsoidal. Foot-layer continuous. Endexine increasing in thickness towards the colpus margins. Sporoderm stratification (EM): Tectum (0.22–0.32 μm thick), columellae (0.18–0.23 μm high), foot-layer (0.05–0.10 μm thick) and endexine (0.06–0.10



Figs. 11–16: Pollen grains of *Eversmannia* (*E. subspinosa*). Fig. 11. Meriodional optical section of endexine shwoing endexine long thinning in equatorial regions, LM × 2000. Fig. 12. Surface view showing lolongate endoaperture, LM × 2000. Fig. 13. Equatorial view showing ruptured area corresponding to endoaperture, SEM × 3250. Fig. 14. Meriodional section of whole pollen grain. Arrows showing thinning of endexine on the middle part of colpus. Exine stratification of colpus margin is distinguished by smooth tectum, reduced foot-layer, granulated or short columellae and thick endexine, TEM × 3800. Fig. 15. Cross section around colpus showing equatorial thinning of endexine, TEM × 12500. Fig. 16. Cross section of mesocolpium showing exine stratification, TEM × 21400.

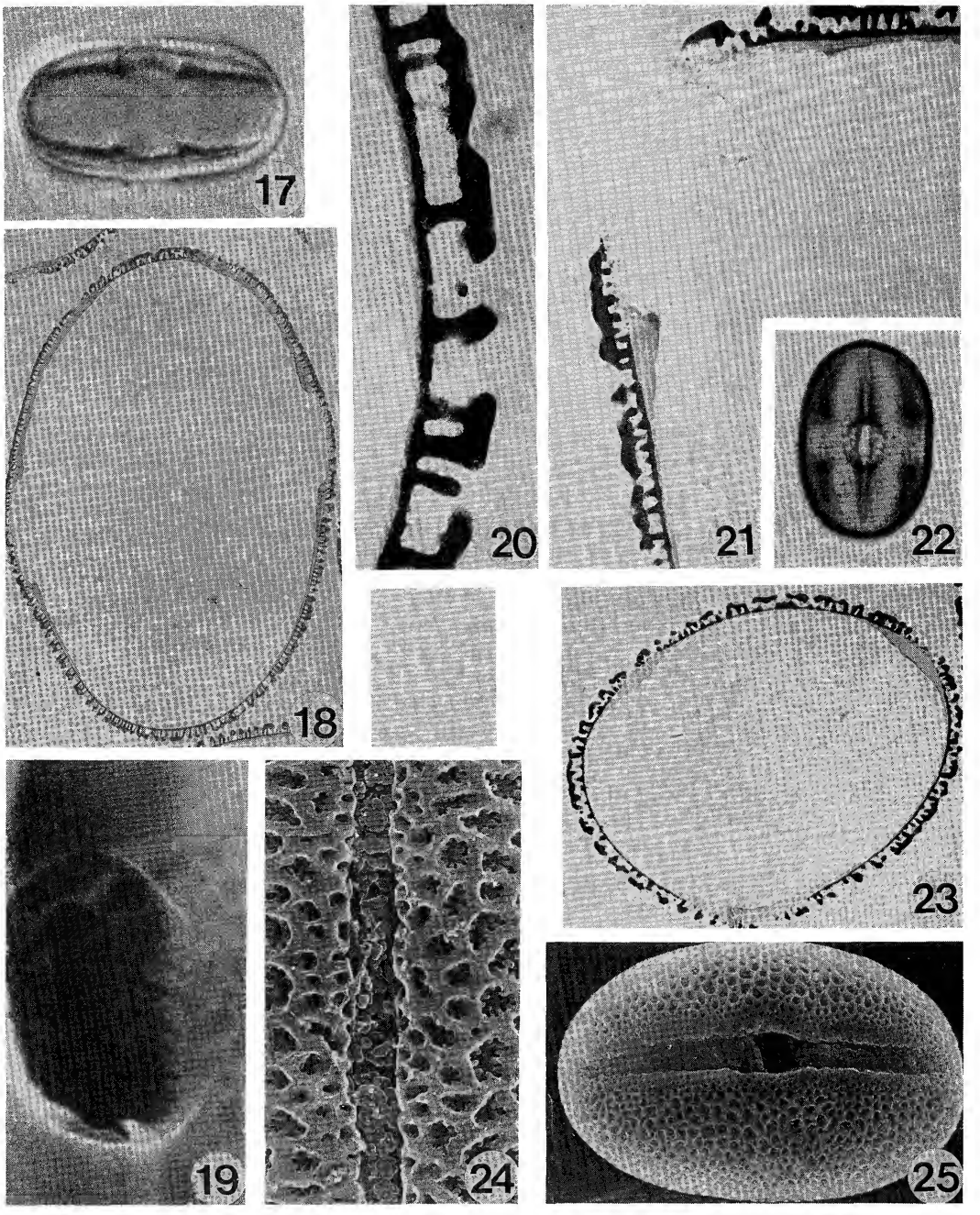
μm thick).

(5-2-2) Sect. **Crinifera** (Boiss.) B. Fedtch. (Figs. 36–39)

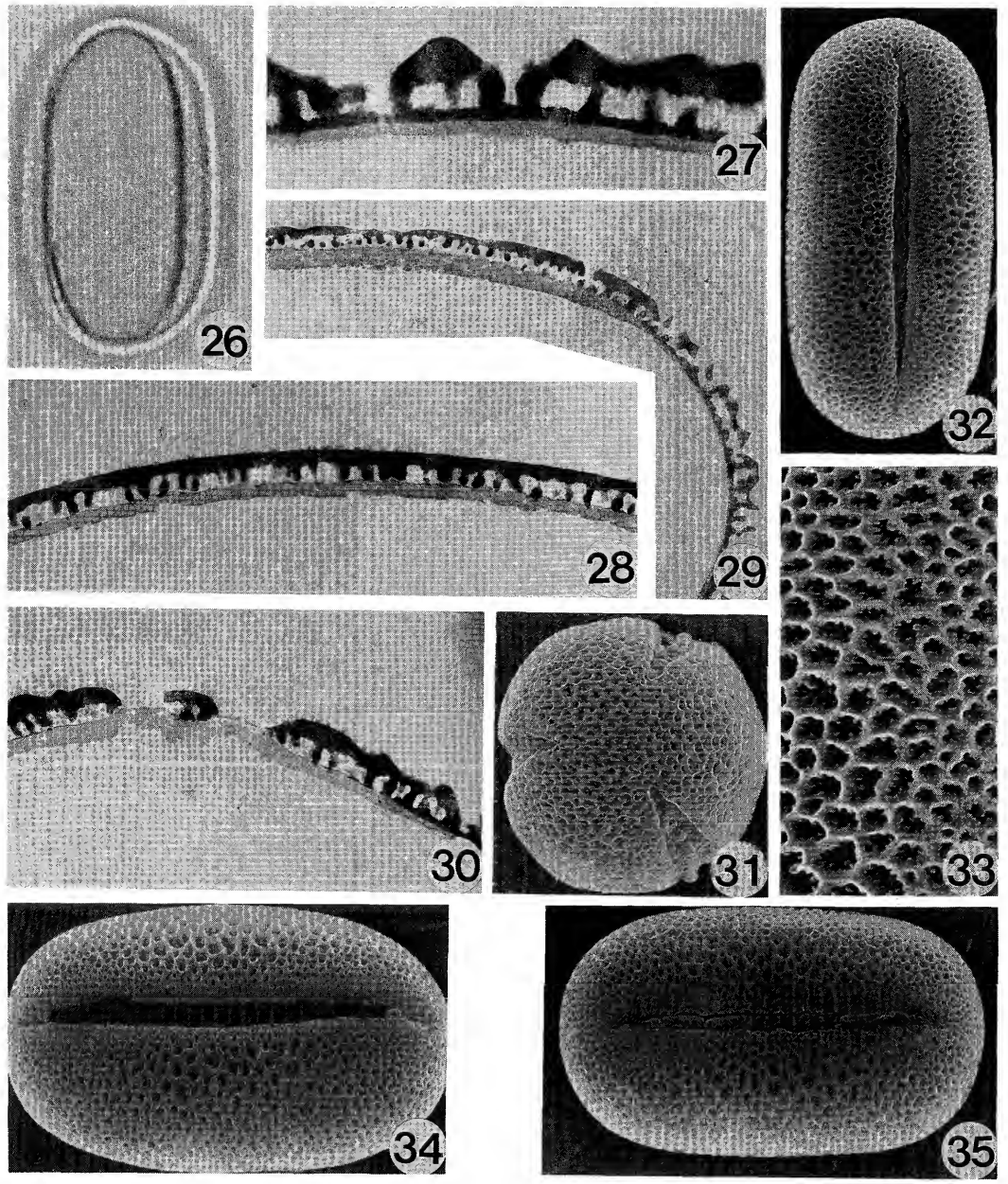
Pollen grains 3-colpate, isopolar, prolate, rounded in polar view, 16.3–19.3 × 9.6–10.7 μm. Colpi long with acute ends, almost reaching the poles, slightly marginate, membrane finely granulated in one row. Exine 0.5–0.6 μm thick, sexine much thicker than the nexine. Tectum evenly reticulate, apocolpium with a sculpture pattern similar to the mesocolpium. Muri relatively wide, distally trapezoidal to keeled, proximally bumpy due to protruded columellae. Lumina rounded to ellipsoidal. Foot-layer continuous. Endexine increasing in thickness towards the colpus margins. Sporoderm stratification (EM): Tectum (ca. 0.2 μm thick), columellae (ca. 0.15-0.20 μm high), foot-layer (0.06–0.08 μm thick) and endexine (0.06–0.08 μm thick).

(5-2-3) Sect. **Membranacea** B. Fedtsch. (Figs. 40–44)

Pollen grains 3-colporoidate, isopolar, prolate to subprolate, rounded in polar view, elliptic in equato-



Figs. 17–25: Pollen grains of *Hedysarum* subgen. Hedysarum. Figs. 17–19: *H. glomeratum*. Fig. 17. Meriodional optical section of endexine showing interruption of the endexine on the pore regions, LM with DIC × 2000. Fig. 18. Meriodional section of whole pollen grain showing interruption of the endexine on the pore regions, TEM × 3400. Fig. 19. Inner view of endoaperture showing interruption of the endexine on the pore regions, SEM × 9000. Figs. 20–24: *H. coronarium*. Fig. 20. Cross section of mesocolpium showing exine stratification, TEM × 22400. Fig. 21. Cross section around pore region showing ora boardered by heavy thickening of endexine, TEM × 8200. Fig. 22. Surface view showing circular endoaperture, LM × 1250. Fig. 23. Cross section of non-pore regions of whole pollen grain showing thick endexine on colpus region, TEM × 4000. Fig. 24. Enlarged the pore region showing densely granulated colpus membranes. Fig. 25. *H. spinosissimum*. Equatorial view showing ruptured area corresponding to pore, SEM × 3000.



Figs. 26–35: Pollen grains of sect. Gamotion in *Hedysarum* subgen. Gamotion. Figs. 26–31: *Hedysarum vicioides* var. *japonicum*. Fig. 26. Meriodional optical section of endexine showing continuous endexine on colpus margins, LM with DIC × 2000. Fig. 27. Cross section of mesocolpium showing exine stratification, TEM × 21900. Figs. 28, 29. Meriodional sections of colpus margin showing uniform thickness of endexine, TEM, × 11400 & × 6700. Fig. 30. Cross section around colpus showing thickening of endexine toward colpus margins, TEM × 13000. Fig. 31. Polar view showing apocolpium with a sculpture pattern similar to the mesocolpium, SEM × 3000. Fig. 32. *H. alpinum*. Equatorial view, SEM × 2750. Fig. 33. *H. limitaneum*. Mesocolpium, reticulate tectum, SEM × 6000. Fig. 34. *H. taoriparium*. Equatorial view showing almost whole colpus membrane ruptured, SEM × 2750. Fig. 35. *H. sikkimense* var. *megalanthum*. Equatorial view showing narrow colpus margins with perforate tectum, SEM × 2500.

rial view, 14.7–18.8 × 12.2–14.5 μm. Colpi long with blunt ends, broad and smooth margins. Colpus membrane coarsely granular in one row. Oroid formed by reducing of the endexine along the polar axis, relatively large, lolongate, 5–6 μm, the membrane corresponding to the endoaperture often not persistent in acetolysed grains. Exine 0.5–0.7 μm thick. Sexine reticulate, about two or three times thicker than the nexine. Muri relatively wide, keeled. Lumina rounded, diminishing in size towards the colpus margins and mesocolpium. Sporoderm stratification (EM): Tectum (0.17–0.26 μm thick), columellae (0.19–0.26 μm high), foot-layer (0.06–0.12 μm thick) and endexine (0.06–0.10 μm thick).

(5-2-4) Sect. **Multicaulia** (Boiss.) B. Fedtsch. (Figs. 45-50)

Pollen grains 3-colpate, isopolar, prolate to perprolate, rounded in polar view, 16.4–23.4 × 9.2–13.1 μm. Colpi long with acute ends, almost reaching the poles, the margins smooth or differentiated from the mesocolpium, the membrane granulated in one row. Exine ca. 0.6 μm thick, sexine much thicker than the nexine. Tectum reticulate, decreasing in size towards the mesocolpium and apocolpium. Muri relatively wide, distally trapezoidal to keeled, proximally bumpy due to protruded columellae. Lumina rounded to ellipsoidal. Foot-layer continuous. Endexine increasing in thickness towards the colpus margins. Sporoderm stratification (EM): Tectum (0.2–0.3 μm thick), columellae (0.14–0.23 μm high), foot-layer (0.06–0.10 μm thick) and endexine (0.06–0.08 μm thick).

(5-2-5) Sect. **Subacaulia** (Boiss.) B. Fedtsch. (Figs. 51–59)

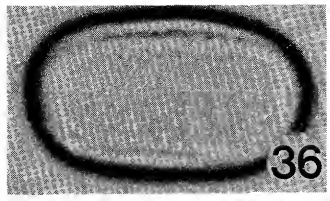
Pollen grains 3-colpate, isopolar, prolate to perprolate, rounded in polar view, 17.7–25.8 × 10.0–16.8 μm. Colpi long with acute ends, almost reaching the poles, with smooth and wide margins, the membrane granulated in one row or operculate. Exine 0.6–0.8 μm thick, sexine two or three times thicker than the nexine. Tectum reticulate or bearing supratectal structure (in *H. lehmannianum*), decreasing in size towards the mesocolpium and apocolpium. Muri relatively wide, distally trapezoidal to keeled, proximally bumpy due to protruded columellae. Lumina rounded to ellipsoidal. Foot-layer continuous. Endexine increasing in thickness towards the colpus margins. Sporoderm stratification (EM): Tectum (0.20–0.35 μm thick), columellae (0.15–0.25 μm high), foot-layer (0.04–0.12 μm thick) and endexine (0.06–0.14 μm thick).

(5-3) Subgen. **Heteroloma** B. Fedtsch. (Figs. 60–67)

Pollen grains 3-colporoidate, isopolar, prolate to subprolate, rounded in polar view, elliptic in equatorial view, 15.9–18.8 × 10.3–12.8 μm. Colpi long with acute ends, broad and smooth margins. Colpus membrane irregularly granular. Oroid formed by reduction of the endexine along the polar axis, relatively large, lolongate, 6–9 μm long, the membrane corresponding to the endoaperture often not persistent in acetolysed grains. Exine 0.5–0.6 μm thick. Sexine finely reticulate, about two times thicker than the nexine. Muri relatively wide, keeled. Lumina rounded, diminishing in size towards the colpus margins and mesocolpium. Sporoderm stratification (EM): Tectum (0.15–0.26 μm thick), columellae (0.18–0.23 μm high), foot-layer (0.04–0.08 μm thick) and endexine (0.06–0.12 μm thick).

(6) **Onobrychis** Miller (Figs. 68–71)

Pollen grains 3-colpate, isopolar, prolate to perprolate, rounded in polar view, compressed oval in equatorial view, 26.2–30.4 × 12.3–15.5 μm. Colpi long with acute ends, narrow margins, the membrane granulated in one row. Exine 0.6–0.8 μm thick. Sexine reticulate, 5 to 6 times thicker than the nexine, muri relatively wide, distally trapezoidal to keeled, proximally bumpy due to protruded columellae. Lumina rounded to ellipsoidal, endexine increasing in thickness towards the colpus margins. Sporoderm stratification (EM): Tectum (0.26–0.30 μm thick), colume-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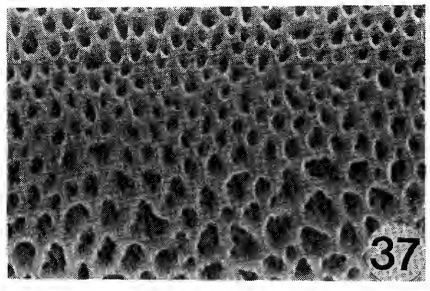
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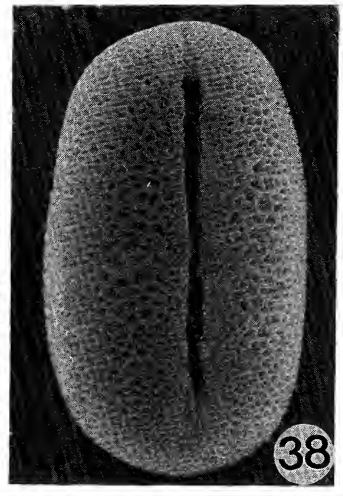
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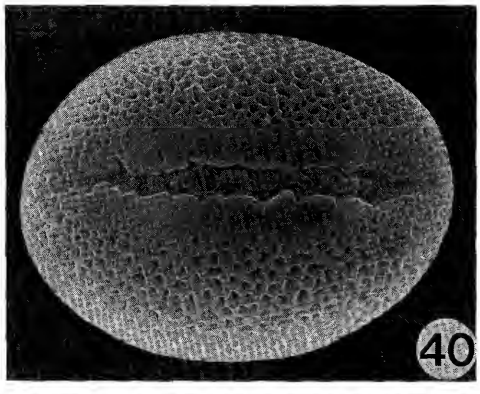
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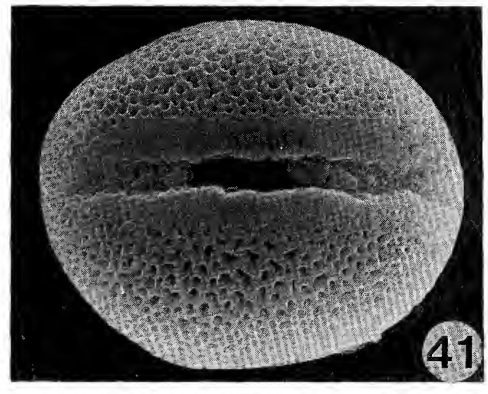
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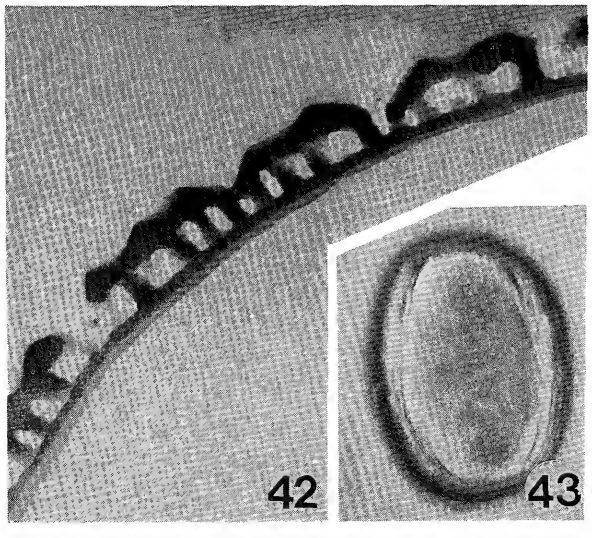
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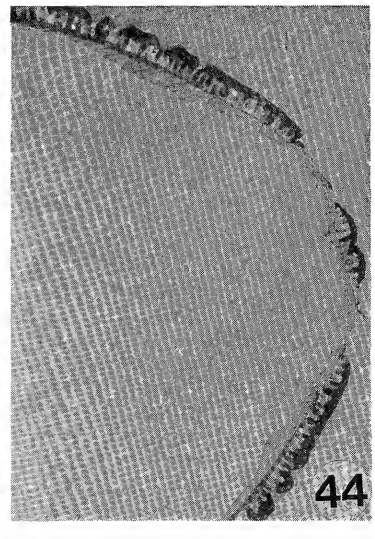
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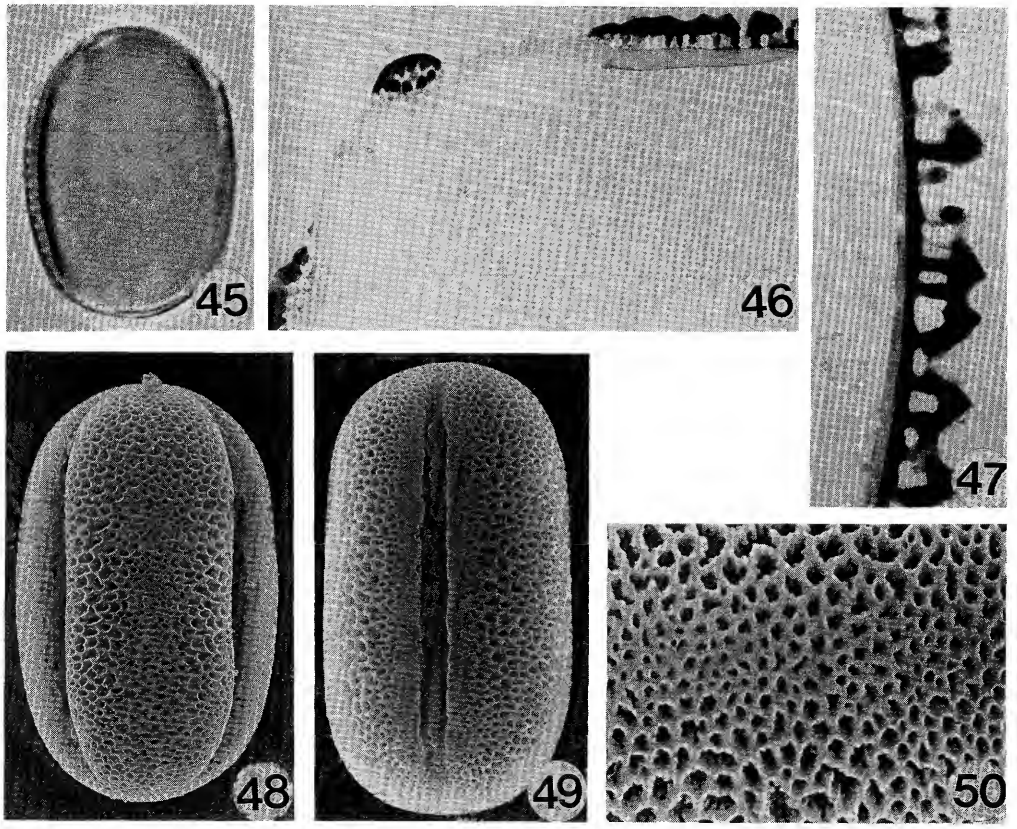


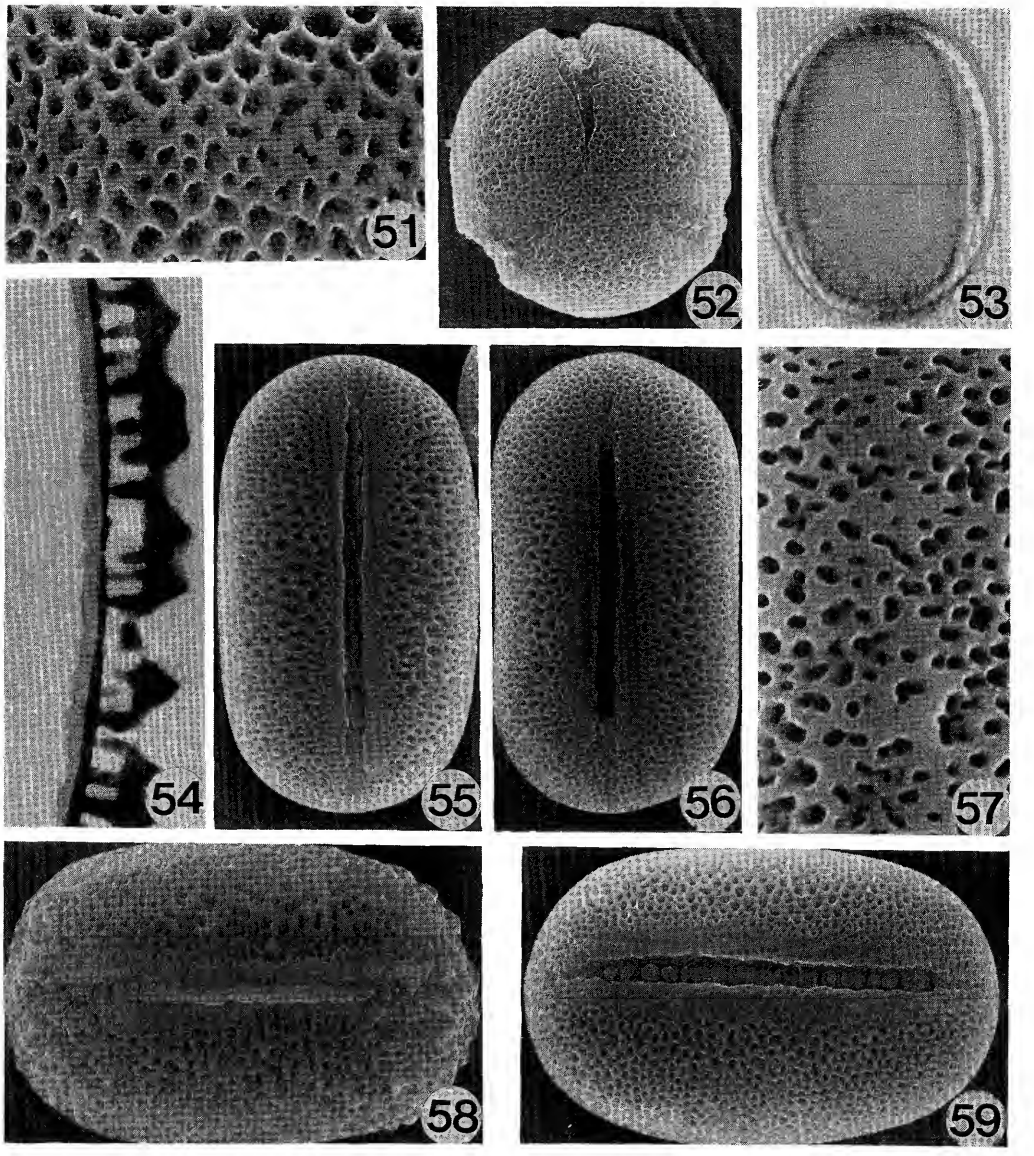
Figs. 45–50: Pollen grains of sect. Multicaulia in *Hedysarum* subgen. Gamotion. Figs. 45–47: *H. brachypterum*. Fig. 45. Meriodional optical section of endexine showing continuous endexine on colpus margin, LM with DIC × 2000. Fig. 46. Cross section around colpus showing thickening of endexine towards colpus margin, TEM × 9700. Fig. 47. Cross section of mesocolpium showing exine stratification, TEM × 18700. Fig. 48. *H. gmelini*. Equatorial view showing almost whole colpus membranes ruptured, SEM × 3250. Fig. 49. *H. razoumovianum*. Equatorial view showing granulate colpus membranes, SEM × 2500. Fig. 50. *H. songolicum*. Mesocolpium showing reticulate tectum and lumina diminishing in size towards mesocolpium, SEM × 7000.

llae (0.30–0.35 μm high), foot-layer (0.07–0.11 μm thick) and endexine (0.01–0.03 μm thick).

(7) **Stracheya** Benth. (Figs. 72–76)

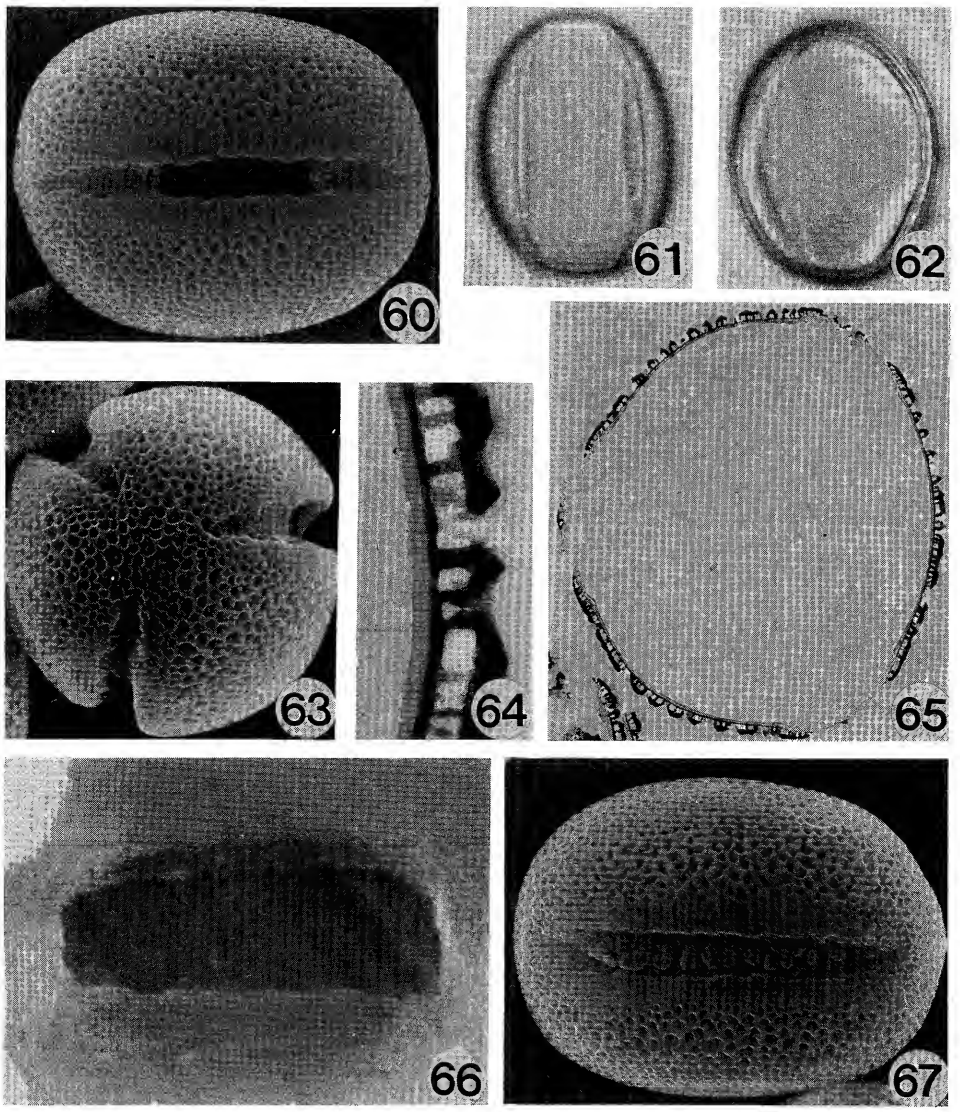
Pollen grains 3-colpate, isopolar, prolate to perprolate, rounded in polar view, 23.6–27.8 × 14.8–17.8 μm. Colpi long with acute ends, narrow margins, the membrane thick and well developed. Exine 0.7–0.9 μm thick. Sexine reticulate, about two times thicker than the nexine. Muri relatively wide, distally trapezoidal to keeled, proximally bumpy due to pro-

Figs. 36–44: Pollen grains of sect. Crinifera (36–39) and sect. Membranacea (40–44) in *Hedysarum* subgen. Gamotion. Figs. 36–39: *H. micropterum*. Fig. 36. Meriodional optical section of endexine showing continuous endexine on colpus margin, LM × 2000. Fig. 37. Mesocolpium showing reticulate tectum and muri proximally bumpy due to protruded columellae, SEM × 7000. Fig. 38. Equatorial view showing almost whole colpus membrane ruptured, SEM × 3250. Fig. 39. Cross section of mesocolpium showing exine stratification, TEM × 20300. Figs. 40–44: *H. membranaceum*. Fig. 40. Equatorial view showing coarsely granulate colpus membranes and reticulate tectum, SEM × 3500. Fig. 41. Equatorial view showing ruptured area corresponding to endoaperture, SEM × 3250. Fig. 42. Cross section of mesocolpium showing exine stratification, TEM × 18000. Fig. 43. Meriodional optical section of endexine showing long thinning endexine in equatorial regions, LM with DIC × 2000. Fig. 44. Cross section around colpus showing equatorial thinning of endexine, TEM × 6000.



Figs. 51–59: Pollen grains of sect. Subacaulia in *Hedysarum* subgen. Gamotion. Fig. 51. *H. cephalotes*. Mesocolpium, reticulate tectum, SEM × 6000. Figs. 52–54: *H. kumaonense*. Fig. 52. Polar view showing apocolpium with a sculpture pattern similar to the mesocolpium, SEM × 2500. Fig. 53. Meriodional optical section of endexine showing continuous endexine on colpus margins, LM with DIC × 2000. Fig. 54. Cross section of mesocolpium showing exine stratification, TEM × 18900. Fig. 55. *H. grandiflorum*. Equatorial view showing granulate colpus membranes, SEM × 2750. Fig. 56. *H. splendense*. Equatorial view showing almost whole colpus membrane ruptured, SEM × 3000. Figs. 57–58: *H. lehmannianum*. Fig. 57. Mesocolpium, SEM × 7000. Fig. 58. Equatorial view showing supratectal structure and well developed colpus membranes, SEM × 2750. Fig. 59. *H. poncinsii*. Equatorial view showing granulate colpus membranes, SEM × 3000.

truded columellae. Lumina rounded to ellipsoidal, decreasing in size towards the mesocolpium or apocolpium. Endexine increasing in thickness towards the colpus margins. Sporoderm stratification (EM): Tectum (0.20–0.35 μm thick), columellae (0.16–0.24 μm high), foot-layer (0.06–0.16 μm thick) and

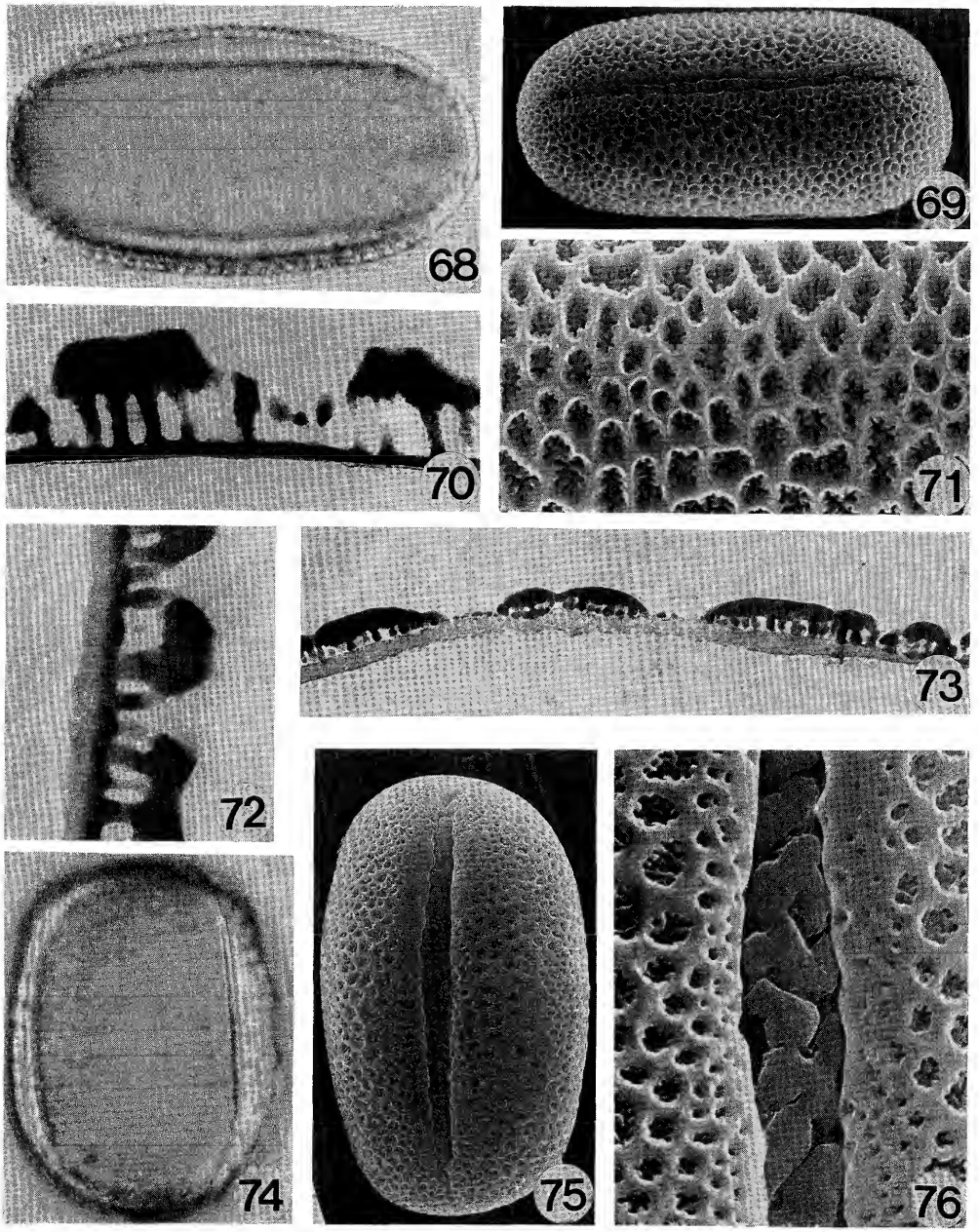


Figs. 60–67: Pollen grains of *Hedysarum* subgen. Heteroloma. Figs. 60–61: *H. multijugum*. Fig. 60. Equatorial view showing ruptured area corresponding to endoaperture, SEM × 3250. Fig. 61. Meriodional optical section of endexine showing long thinning endexine on colpus region, LM with DIC × 2000. Figs. 62–67: *H. fruticosum*. Fig. 62. Meriodional optical section of endexine showing long thinning endexine on colpus region, LM with DIC × 2000. Fig. 63. Polar view showing apocolpium with a sculpture pattern similar to the mesocolpium, SEM × 3250. Fig. 64. Cross section of mesocolpium showing exine stratification, TEM × 17100. Fig. 65. Cross section of whole pollen grain, TEM × 3300. Fig. 66. Inner view of endoaperture showing long thinning of endexine on colpus margins, SEM × 5000. Fig. 67. Equatorial view showing coarsely granulate colpus membranes, SEM × 3250.

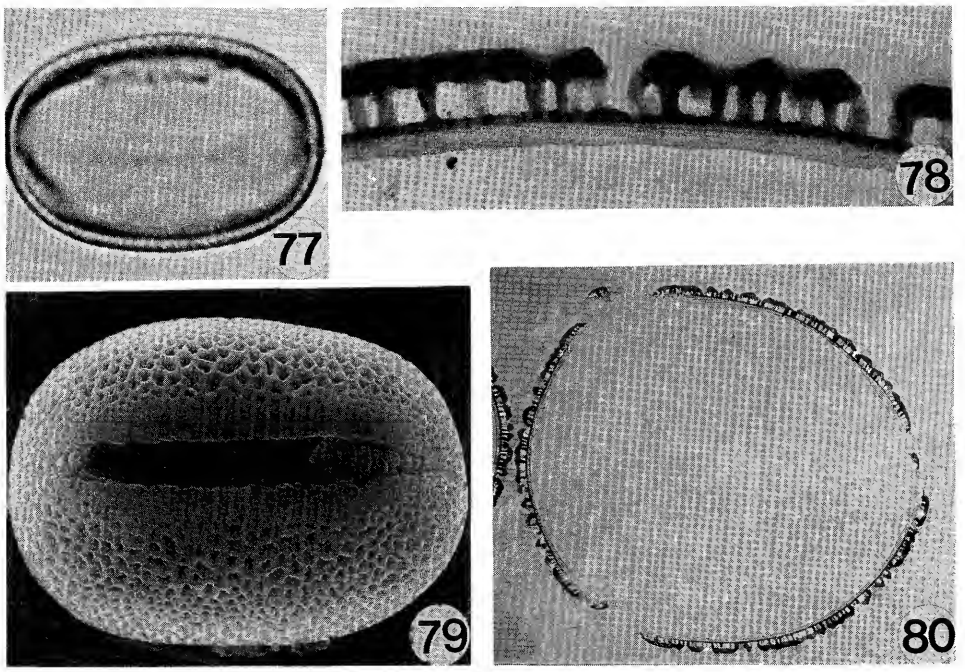
endexine (0.06–0.15 μm thick).

(8) **Taverniera** DC. (Figs. 77–80)

Pollen grains 3-colporoidate, isopolar, prolate to subprolate, rounded in polar view, elliptic in equatorial view, 16.9–18.8 × 11.9–13.5 μm. Colpi long with acute ends, broad and smooth margins. Colpus membrane irregularly granular. Oroid formed by reduction of the endexine along the polar axis, relatively large,



Figs. 68–76: Pollen grains of *Onobrychis* (68–71) and *Stracheya* (72–76). Figs. 68–71: *Onobrychis oxyodenta*. Fig. 68. Meriodional optical section of endexine showing continuous endexine on colpus margins, LM with DIC × 2000. Fig. 69. Equatorial view showing granulate colpus membranes in one row, SEM × 1850. Fig. 70. Cross section of mesocolpium showing sexine much thicker than nexine and thin endexine, TEM × 20000. Fig. 71. Mesocolpium showing muri keeled, SEM × 6000. Figs. 72–76: *Stracheya tibetica*. Fig. 72. Cross section of mesocolpium showing exine stratification, TEM × 20000. Fig. 73. Cross section around colpus showing thickening of endexine towards colpus, TEM × 8400. Fig. 74. Meriodional optical section of endexine showing continuous endexine on colpus margin, LM × 2000. Fig. 75. Equatorial view, SEM × 2150. Fig. 76. Enlargement of colpus showing well developed colpus membranes and keeled muri, SEM × 6000.



Figs. 77–80: Pollen grains of *Taverniera* (*T. nummularia*). Fig. 77. Meriodional optical section of endexine showing long thinning endexine in equatorial region, LM × 2000. Fig. 78. Cross section of mesocolpium showing exine stratification, TEM × 20800. Fig. 79. Equatorial view showing ruptured area corresponding to endoaperture, SEM × 3250. Fig. 80. Cross section of whole pollen grain, TEM × 3000.

lolongate, about 9 μm long, the membrane corresponding to the endoaperture often not persistent in acetolysed grains. Exine 0.5–0.7 μm thick. Sexine reticulate, about two times thicker than the nexine. Muri relatively wide, keeled. Lumina rounded, diminishing in size towards the colpus margins and mesocolpium. Sporoderm stratification (EM): Tectum (0.15–0.25 μm thick), columellae (0.15–0.25 μm high), foot-layer (0.04–0.08 μm thick) and endexine (0.10–0.20 μm thick).

Summarized description of pollen morphology of Hedysareae

Monad, isopolar, tricolpate or less frequently tricolporoidate or tricolporate, mostly prolate, rarely subprolate or perprolate, 14–30 μm in polar length, and more or less circular in polar view.

Colpi long with acute ends, almost reaching the poles, narrow, membrane granulate to operculate, and with smooth to perforate sculpture margins. Exine 0.4–0.9 μm thick, tectate and columellate. Foot-layer continuous, distinct, and relatively thin around the apertural regions. Extexine reticulate to perforate, smaller in the middle of the mesocolpia and apocolpia. Occasional small processes in many lumina. Endexine usually as thick as the foot-layer in the mesocolpia, increasing in thickness towards the apertural regions, but decreasing towards the polar regions.

Discussion

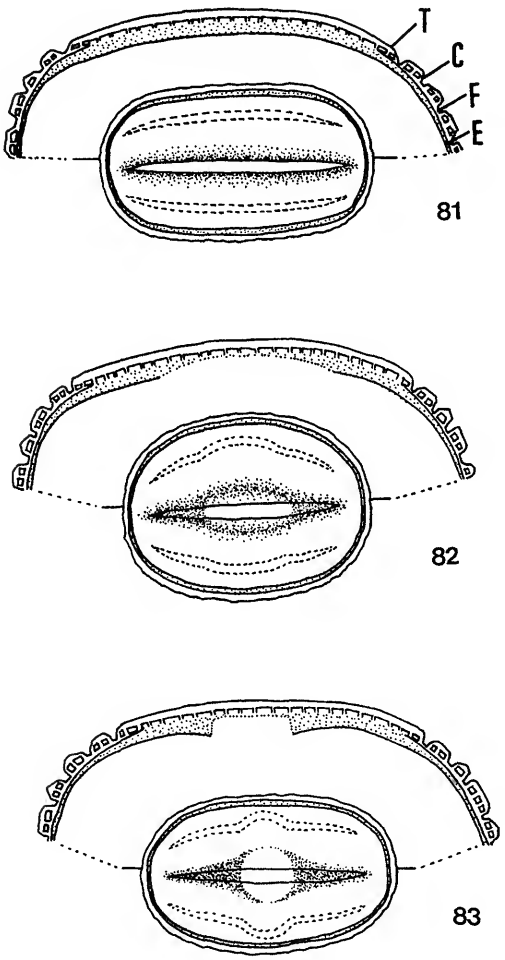
Pollen types

Endexine thickness around the apertural regions shows clear differences in the tribe Hedysareae. The following three types of pollen grains are recognized:

1) Tricolpate type (Fig. 81): Pollen grains have three colpi, the endexine neither reduced nor thinned at the equatorial region. Almost the entire colpus

membrane is often ruptured by acetolysis treatments.

2) Tricolporoidate type (Fig. 82): Pollen grains have three colpi and oroids. The oroid is clear or obscure and bordered by weak thickening of the endexine along the polar axis.



Figs. 81–83: Diagrammatic illustrations of three pollen types of the tribe Hedysareae. Fig. 81. Tricolpate pollen grain, the endexine is not reduced or thinned on any regions of the colpus margin. Fig. 82. Tricolporoidate pollen grain, the endexine is thinned in the middle of the colpus to form a lolongate endoaperture. Fig. 83. Tricolporate pollen grain, the endexine is markedly reduced in its thickness at the equator to form a circular endoaperture. In each figure, the upper one shows the meriodional section along the colpus margin. Exine stratification of the colpus margin is distinguished by a smooth tectum (T), short or granulated columellae (C), reduced foot-layer (F) and thick endexine (E). Dotted area in each of the lower figures indicates that of the thickened endexine.

3) Tricolporate type (Fig. 83): Pollen grains have three colpi and ora. The ora are circular and are formed by an interruption of the thick endexine in the equatorial region.

Distribution of pollen types in Hedysareae

(1) Tricolpate type

This pollen type is the most common in the tribe Hedysareae. It was found in all perennial herbaceous groups as *Ebenus, Onobrychis, Stracheya* and the four sections Crinifera, Gamotion, Multicaulia and Subacaulia of the subgenus Gamotion in the genus *Hedysarum*. Morphological distinctions among the four sections were pointed out as confusing by Rollins (1940). As opposed to these sections, the remaining section Membranacea is characterized by suffrutescent stems and tricolporoidate pollen.

The pollen morphology of the four sections is, moreover, quite similar to each other in having tricolpate aperture structures, granular or rod form colpus membranes in a row, reticulate tectum and features in exine stratification. However, they differ slightly in pollen size; the mean value of pollen sizes are Crinifera (17.9 μm), Gamotion (21.1 μm), Multicaulia (19.4 μm) and Subacaulia (20.5 μm) (Table 1).

The pollen grains of *Hedysarum lehmanianum* of the section Subacaulia are distinctive in having supra tectal structure (Fig. 58). Guinet and Ferguson (1989) reported the sporadic occurrence of this structure in remotely related groups in Leguminosae and noted that the structure is associated with large pollen grains in *Bauhinia, Macrotyloma* and *Herpyza*. The pollen size of *H. lehmanianum* seems to be slightly larger (20.2–25.8 × 13.6–16.8 μm) than that of other species in the section (their sizes vary 17.7–24.0 × 10.0–14.5 μm). The phylogenetic significance of this structure is not considered in this study, because it was observed only in one species in the tribe. The supratectal structure appears to be an autoapomorphic characteristic for *H. lehmanianum*.

Stracheya tibetica, a species of the monotypic genus, occurs in high altitude regions of the Himalayas and has been distinguished from *Hedysarum* by its fruit with prickles. The species is very similar to those of section Subacaulia of the subgenus Gamotion in *Hedysarum* in flower structure and dwarf habit. Pollen morphology of *S. tibetica* was recorded as quite similar to that of *Corethrodendron, Ebenus* and *Hedysarum* (Ohashi 1971). The pollen grains of *S. tibetica* are similar to those of the section Gamotion in tricolpate aperture structure, exine stratification and tectum sculpture. However, the former grains differ from the latter in having thicker exine (0.7–0.9 μm thick; Fig. 72), well developed colpus membranes (Figs. 75–76), larger size (23.6–27.8 μm) and the lumina sculpture with developed intectate columellae. The pollen grains of *S. tibetica* differ from those of *Corethrodendron* and *Ebenus* in having the colpus membranes in a row and a thick exine.

Ebenus and *Onobrychis* are closely allied and are distinguished from *Hedysarum* by having fruits which are not jointed with 1 or 2 seeds (Polhill 1981). The pollen grains of the two genera are similar to that of perennial groups of *Hedysarum* and *Stracheya* in having colpate aperture structures and reticulate tectum, but are different in shape, i.e., perprolate vs. prolate in *Hedysarum*. Moreover, pollen grains of *Onobrychis* are distinguished from those of *Hedysarum* and *Ebenus* in having an exdexine much thinner than the foot-layer (Fig. 70). The pollen morphology of *Ebenus* is similar to *Hedysarum* in wall stratifications and is similar to *Onobrychis* in size and shape, but differs from the latter two genera in having a thicker exine (0.8–0.9 μm). More species of *Onobrychis* need to be examined for a discussion of the pollen morphological relations between these two genera.

(2) Tricolporate type

The tricolporate pollen grains have three apertures composed of colpi and ora which are formed by the abrupt interruption of the thick endexine in the equatorial areas (Figs. 17–19, 83). The characteristics of densely granular colpus membranes (Fig. 24), higher columellae (Fig. 20) and clear circular endoaperture are quite different from other pollen types of Hedysareae. This pollen type was recognized only in the species of section Hedysarum of *Hedysarum*.

The species of this section are distinct from other species of the genus in habitat growing on seashores of the Mediterranean, and in having free stipules and an annual habit.

Ferguson and Skvarla (1981) already described the pollen of the section Hedysarum as tricolporate and assigned it as similar to that of the tribe Coronilleae. Pollen wall stratification with thinner endexine, continuous foot layer, higher columellae and thinner tectum of the section Hedysarum is, however, clearly different from pollen grains of Coronilleae. The pollen morphology of the section Hedysarum is not allied with that of the tribe Galegeae described by Ferguson and Skvarla (1981).

(3) Tricolporoidate type

Tricolporoidate grains have three apertures composed of colpi and indistinct ora, oroid (Erdtman 1966), which are endoapertures formed by the reduced endexine in the equatorial area (Figs. 14, 66, 82), and also have characteristics of pollen shape (subprolate or prolate), tectum sculpture (finely reticulate to reticulate) and smaller size (13.2–18.8 μm).

The pollen grains with tricolporoidate apertures were observed in all the shrubby groups of *Alhagi, Corethrodendron, Eversmannia, Hedysarum* (subgenus Heteroloma and section Membranacea in the subgenus Gamotion) and *Taverniera* in the present study. The pollen grains *Alhagi* and *Eversmannia* have more or less clear and short endoapertures (Figs. 1, 11–13), while those of *Corethrodendron, Hedysarum* (subgenus Heteroloma and section Membranacea in the subgenus Gamotion) and *Taverniera* have diffuse endoapertures which are a

long reduction of the endexine along the polar axis (Figs. 4–6, 41, 61, 66, 77, 79). Pollen grains of the latter groups were regarded to be tricolpate in previous studies (Ohashi 1971, Ferguson and Skvarla 1981).

Alhagi has generally been classified into Hedysareae by Candolle (1825), Bentham (1865), Hutchinson (1964) and Ohashi (1971). However, Polhill (1981) treated the genus in the tribe Galegeae on the characteristic of fruits with obscure septum. Sanderson and Liston (1995) suggested recently that *Alhagi* is closer to Hedysareae than Galegeae based on molecular evidence. Morphology of flowers and fruits shows that *Alhagi* is transitional between Hedysareae and Galegeae (Choi 1988). *Alhagi* appears to be allied to *Eversmannia* by its floriferous spines, ovaries and fruits (Polhill 1981, Choi 1988).

Pollen grains of *Eversmannia* are very similar to those of *Alhagi* in the following characters: a more or less clear and short endoaperture, subprolate to prolate in shape and perforate to finely reticulate in tectum sculpture. Also, these pollen grains are the shortest in Hedysareae. The aperture structure, wall stratification and exine sculpture of pollen grains of these genera are different from those of tricolporate pollen of the section Hedysarum of *Hedysarum* and tricolporoidate pollen observed in *Corethrodendron*, subgenus Heteroloma of *Hedysarum* and *Taverniera*.

Taverniera has been distinguished from *Hedysarum* in having few leaflets (1- to 3-foliolate). Recently, the separation is regarded to be artificial (Polhill 1981, Thulin 1985), because some species of the section Subacaulia of *Hedysarum* are also 1–3-foliolate. Furthermore, *Taverniera* is closely allied to *Hedysarum* subgenus Heteroloma in gross morphology (Polhill 1981, Thulin 1985). The pollen morphology of *Taverniera* is also similar to that of the subgenus Heteroloma of *Hedysarum*.

Corethrodendron subspinosa is the sole species of this monotypic genus and is distinguished from *Hedysarum* by the characteristic of inflated fruits. It has been treated as a species of *Hedysarum* by Fedtschenko (1902, 1948) and Polhill (1981). The fruits of *C. subspinosa* are not different from those of the subgenus Heteroloma of *Hedysarum* (Choi 1988). Also, the pollen grains of *C. subspinosa* is very similar to that of *Hedysarum* subgenus Heteroloma.

Pollen grains of subgenus Heteroloma are more similar to those of *Taverniera* and *Corethrodendron* than those of subgenera Hedysarum and Gamotion. Evidence from pollen morphology, therefore, supports that segregation of the two genera from *Hedysarum* subgenus Heteroloma is of no significance.

The section Membranacea of the subgenus Gamotion in *Hedysarum* is composed of only one species, *H. membranaceum*, which is distributed in a limited area of northwest Africa. In Gamotion, Membranacea is distinguished from the remaining four sections by the characteristics of the suffrutescent stem, flowers and fruits. Distribution is also distinct. The pollen of Membranacea apparently differs from the other sections by its tricolporoidate aperture structure, smaller size, and prolate to subprolate shape (Figs. 40–44). Aperture structures are similar to those of shrubby groups of *Corethrodendron*, subgenus Heteroloma of *Hedysarum* and *Taverniera*. However, the reticulate tectum sculpture of section Membranacea is more similar to that of members of the four sections of the subgenus Gamotion than those of two genera and the subgenus Heteroloma.

Specialization of pollen morphology in Hedysareae

Tricolpate pollen is supposed to be derived from tricolporate pollen and reticulate tectum sculpture may have originated from perforate in Papilionoideae (Guinet 1981, Ferguson and Skvarla 1981). Polhill (1981) suggested that the tribe Hedysareae is derived from the tribe Galegeae based on evidence from habitat and flower structure. The pollen of Galegeae has a tricolporate aperture with predominantly perforate or finely reticulate exine sculpture, while the

most common pollen of Hedysareae has a tricolpate aperture with reticulate exine, as shown in the present study. Accordingly, the most common pollen of Hedysareae is inferred to be derived from that of Galegeae.

Alhagi has been considered to be intermediate between Hedysareae and Galegeae and is closely allied to *Eversmannia* (Polhill 1981). The genus is considered to be the most primitive in Hedysareae on the basis of fruit and flower structure (Choi 1988). Therefore, the tricolporoidate pollen with perforate tectum of *Alhagi* and *Eversmannia* might be the most primitive type in Hedysareae. Then, such a primitive type of pollen grain must evolve into the advanced tricolpate pollen grains with reticulate tectum sculpture in Hedysareae. The evolution of the endoaperture is inferred to be the thinning of the endexine beneath the colpi from the equatorial area (tricolporoidate, Fig. 82) to polar regions (colpate, Fig. 81), as already described in Leguminosae by Ferguson and Skvarla (1981). This trend in endoaperture is associated with specialization in tectum sculpture (perforate to reticulate), pollen shape (subprolate or prolate to perprolate), colpus membrane (granular to operculum) and larger pollen size. That is, the most advanced pollen is inferred to be the tricolpate type with reticulate tectum, larger size, prolate shape and operculate colpus membranes in Hedysareae, which is observed in *Hedysarum* (sections Crinifera, Gamotion, Multicaulia and Subacaulia in the subgenus Gamotion), *Stracheya, Ebenus* and *Onobrychis*. This pollen trend also agrees with the broad trend from macromorphology in the tribe, particularly with the specialization in habit and flower and fruit structures (Choi 1988).

The other trend in aperture structures is the formation of a circular endoaperture (colporate) due to thickened endexine, 'negative annuls' (Guinet and Ferguson 1989) which was observed in the species of section Hedysarum (Figs. 17–25, 83). The pollen characters of the section, which are extremely thin exdexine, columellae about three times thicker than foot-layer and reticulate tectum sculptures, are not allied to those of the tricolporate type of the Galegeae in having thicker exdexine, columellae slightly thicker than foot-layer and perforate ones which were observed on *Astragalus* and *Glycyrrhiza* (Ferguson and Skvarla 1981). Therefore, this pollen might be derived from the tricolporoidate pollen of the Hedysareae by thickening of the endexine in the equatorial area, which is a reversal of the trend to tricolpate.

Conclusions

1. Three pollen types were recognized in the tribe Hedysareae, i.e. tricolporate, tricolporoidate and tricolpate, and the tricolpate type with reticulate tectum was the most common in the tribe.

2. In Hedysareae, the tricolporoidate aperture (oroid) was inferred to be changed into tricolpate aperture by reduction of the endexine or to tricolporate by thickening of the endexine in the equatorial areas. This evolutionary trend in the endoaperture was associated with specializations in the tectum sculpture (perforate to reticulate), colpus membranes (granules to operculum), shape (subprolate to prolate) and size (small to larger).

3. The pollen grains of *Alhagi* and *Eversmannia* are very similar in having tricolporoidate apertures and a perforate tectum. They were inferred to be the most primitive type in Hedysareae.

4. Pollen characteristics of *Hedysarum* subgenus Heteroloma are more related to the genera *Taverniera* and *Corethrodendron* than to the other infrageneric groups of *Hedysarum*. This fact is supported by evidence from macromorphological characters.

5. The pollen of *Stracheya* is similar to that of perennial species of subgenus Gamotion.

6. The pollen morphology of *Onobrychis* and *Ebenus* differs from that of *Hedysarum* in size and shape, and pollen of *Onobrychis* has distinctive characteristics in wall stratification from other genera.

7. The pollen of subgenus Hedysarum has tricolporate apertures and was different from that of other members of *Hedysarum* as well as the tribe Hedysareae. This difference corresponds to the distinctive characteristics of the section in habit, distribution pattern and stipule morphology.

8. In subgenus Gamotion of *Hedysarum*, except section Membranacea, the pollen type of sections Crinifera, Gamotion, Multicaulia, and Subacaulia is tricolpate in aperture, reticulate in sculpture and with a thin endexine, narrow foot layer, long columellae and thick tectum in wall stratification. The type is most common in the tribe.

9. In the subgenus Gamotion, the pollen morphology of the section Membranacea was different from the other four sections in having a tricolporoidate aperture and smaller grains. The differences correspond to that of the habitat, the flower and fruit structures and the distribution pattern.

10. The pollen characteristics support the infrageneric system of *Hedysarum* proposed by Fedtschenko (1902) in part, but provide no substantial basis for separating *Corethrodendron*, *Stracheya* and *Taverniera* from *Hedysarum* as distinct genera.

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Endnote

Subgen. **Gamotion** (Basiner) B. Choi & H. Ohashi, **stat. nov.** Lectotype: *H. alpinum* L. (= *H. elongatum* Fisch.).

Sect. Gamotion Basiner in Bull. Acad. St.-Pétersb. **4**: 311 (1845); Chrtkova-Zertova in Fl. Europ. **2**: 186 (1968). Lectotype: *H. alpinum* L.

Trib. Isoloma Basiner sect. Gamotion Basiner in Bull. Acad. St.-Pétersb. **4**: 310 (1845); Boiss., Fl. Orient. **2**: 512 (1872), nom. illeg.

Subgen. Isoloma B. Fedtsch. trib. Gamotion (Basiner) B. Fedtsch. in Bull. Herb. Boiss. **7**: 256 (1899), nom. illeg.

Trib. Isoloma subtrib. Gamotion B. Fedtsch., Hedys. 208 (1902), nom. illeg.

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Appendix I: List of species and specimens examined with their pollen characteristics and/or pollen size.

(1) **Alhagi**

A. maurorum Medik.

W. Pakistan, Gulistan, 28 May 1955, S. Kitamura s.n. (TI).

Pollen size 13.2–15.2 × 10.7–12.0 μm.

(2) **Corethrodendron**

C. scoparium Basiner

China, Prov. Hsingan, 12 Aug. 1936, Kitagawa s.n. (TI); China, Tatsingshan, Liu 98 (PE).

Pollen size 15.0–17.7 ×10.3–12.2 μm.

(3) **Ebenus**

E. sibthorpii DC.

Attika, near Athens, 20 June 1861, L. Leutwein de Fellenberg s.n. (KYO).

Pollen size 25.0–28.0 × 11.6–14.0 μm.

(4) **Eversmannia**

E. subspinosa (DC.) B. Fedtsch.

Afghanistan, 27 May 1884, Aitchison 574 (BM); Songaria, Chrenk s.n. (BM).

Pollen size 15.0–17.2 × 10.8–12.2 μm.

(5) **Hedysarum**

(5-1) Subgenus **Hedysarum**

H. coronarium Linn.

Siciley, P. Davis and D. S. Sutton 64330 (BM); Spain, Cadiz, C. A. Walker 95 (BM).

Pollen size 21.5–24.1 × 10.5–13.6 μm.

H. glomeratum F. G. Dietrich.

Sicily, 24 March 1931, Mery Heard s.n. (BM); Sardinia, Capo Figara, Humphrico and Richardson 135 (BM).

Pollen grains have smooth and wide colpus margins and granular colpus membranes in one row. Sporoderm stratification (EM): Tectum (0.14–0.20 μm thick), columellae (0.17–0.25 μm high), foot-layer (0.05–0.08 μm thick), endexine (0.04–0.08 μm thick). Pollen size 17.7–19.2 × 9.8–11.7 μm.

H. spinosissimum Linn.

Spain, Isl. Baleares, J. F. M. and M. J. Cannon 3954 (BM); Spain, Prov. Almeria, M. F. and S. G. Gardner 1592 (BM).

Pollen grains have coarsely granular colpus membranes, smooth and wide colpus margins. Pollen size 18.4–20.9 μm in polar length.

(5-2) Subgen. **Gamotion** (Basiner) B. Choi & H. Ohashi

(5-2-1) Section **Gamotion** Basiner

H. alpinum L.

China, Werleurkakaju, Turzaninow s.n. (E); China, Hsinganling, K. Yamatsuta 158 (TI); Dahuria, Karo s.n. (E); China, Hsingan-ling, 29 July 1930, Kitagawa s.n. (TI).

H. austrosibiricum Fedtsch.

USSR, Kazachstania, 27 July 1963, S. Arystangaliev s.n. (E).

Pollen size 19.8–22.8 × 10.2–11.9 μm.

H. cachemirianum Benth. ex Baker.

India, Kashmir, T. A. Rao 9552 (TI).

H. campylocarpon H. Ohashi.

Nepal, Langtang, O. Polunin 562 (TI).

H. citrinum E. G. Baker.

Tibet, Konbo, F. Ludlow et al. 13954 (TI).

Pollen grains have colpus with well developed operculate membranes and lumina rounded. Pollen size 19.7–22.1 × 11.8–12.1 μm.

H. falconeri Baker.

Karakoram, B. S. Russell 1109 (TI).

H. fistulosum Hand.-Mzt.

China, Yunnan, G. Forrest 17621 (E).

Pollen size 22.8–25.8 × 12.7–14.5 μm.

H. hedysaroides (L.) Schniz & Thell

Japan, Taisetu-san, Aug. 1928, T. Nakai s.n. (TI); Japan, Isl.

Rebun, H. Takahashi 4316 (TUS); Japan, Mt. Nakko-dake, H. Hara 3731a (TI).

H. inundatum Turcz.

China, Hsiaowutaishan, T. P. Wang 594 (E).

Pollen grains have muri extremely bumpy due to protruded columellae and has colpus with microperforate margins and finely granulate membranes.

Pollen size 17.0–19.0 × 11.1–13.5 μm.

H. limitaneum Hand.-Mzt.

W. China, F. Kingdon Ward 584 (E).

Pollen size 20.1–22.4 × 11.8–14.0 μm.

H. limprichtii Ulbr.

China, Szechuan, R. Cunnigham 186 (E).

Pollen size 20.9–23.4 × 12.1–14.1 μm.

H. manaslense var. *nepalense* H. Ohashi.

Nepal, Taglung, Stainton et al. 1698 (TI).

H. sachalinense Fedtsch.

USSR, Sachaline, H. Hara 899a and 899c (TI); Etorofu-to, 7 Aug. 1928, Saito s.n. (TI); Isl. Shikotan, 15 July 1930, S. T. Ono s.n. (TI); Isl. Shikotan, 4 Aug. 1923, K. Kondo s.n. (TI).

Pollen size 18.5–21.0 × 11.5–13.4 μm.

H. semenowii Regel & Herder.

USSR, Kazachstania, 10 July 1964, I. Roldugins s.n. (E).

Pollen grains have colpus with smooth and broad margins and with well developed membranes. Pollen size 17.9–19.9 × 10.3–11.8 μm.

H. sikkimense Benth. ex Baker.

E. Nepal, Lama Chungbu, 24 June 1972, H. Kanai et al. s.n. (TI).

H. sikkimense var. *megalanthum* H. Ohashi & Tateishi.

W. China, F. Kingdon Ward 858 (E).

Pollen size 19.7–22.3 × 10.7–12.3 μm.

H. taoriparium B. Choi & H. Ohashi.

China, Kansu, T'ao River basin, J. F. Rock 12623 (E).

Pollen grains have smooth and wide colpus margins and has colpus membrane often not persistent in acetolysed grains. Pollen size 20.6–22.5 μm in polar length.

H. tuberosum Fedtsch.

China, Kansu, R. Farrer and W. Purdom 105 (E).

Pollen size 20.5–24.3 × 10.8–13.0 μm.

H. vicioides var. *chinense* B. Choi & H. Ohashi.

China, Mts. Tatsingshan, Ma et al. 7 (TUS); China, Mts. Hsiaowutaishan, Wang 766 (TUS).

H. vicioides var. *japonicum* f. *japonicum* (Fedtsch.) B. Choi & H. Ohashi.

Japan, Mt. Zao, Choi 369 (TUS); Mt. Iide, Nakahara s.n. (TUS); Mt. Yukikuradake, Chen and Inoue s.n. (TUS); Mt. Yubaridake, Hara 2930b (TI); Mt. Fuji, S. Noshiro 3543 (TUS); Mt. Fuji, Y. Tateishi 2266 (TUS); Korea, Mt. Paekdu, Mori 79 (TI); Korea, Mt. Kwanmo, Nakai 7205 (TI).

H. vicioides var. *japonicum* f. *pilosum* (Ohwi) Kitagawa.

Japan, Mt. Kitadake, H. Iketani 1013 (TUS); USSR, Prov. Primorje, N. Pavlova 5684 (E).

(5-2-2) Section **Crinifera** (Boiss.) B. Fedtsch.

H. micropterum Bunge.

Transcaspica, Kisil Arwat, Karakola, P. Sintenis 1804 (E); Freyn s.n. (E).

Pollen size 16.3–19.3 × 9.6-10.7 μm.

(5-2-3) Section **Membranacea** B. Fedtsch.

H. membranaceum Coss. & Bal.

Moroco, Goodchild 62 (BM).

Pollen size 14.7–18.8 × 12.2–14.5 μm.

(5-2-4) Section **Multicaulia** (Boiss.) B. Fedtsch.

H. brachypterum Bunge.

China, M. Togashi 726 (TUS); China, Akagi 15 (TI).

Pollen size 17.3–20.3 × 9.8–11.4 μm.

H. gmelini Led.

Altai merid, 22 July 1930, P. Smirnow s.n. (E); China, 1959, Mongmu Xi Yuan 6 (TUS).

Pollen grains have colpus membrane often not persistent in acetolysed grains. Pollen size 17.0–19.7 × 10.2–11.6 μm.

H. hemithamnoides Korot.

USSR, Tadzhikistania, M. Popov and A. Vvedensky 6247 (E).

Pollen grains have the well developed colpus membranes. Pollen size 16.4–18.4 × 10.0–12.2 μm.

H. iomuticum Fedtsch.

USSR, Uzbekistania, V. Botschantzev and A. Vvedensky s.n. (E).

Pollen grains have more thicker muri. Pollen size 19.8–23.1 × 9.6–12.5 μm.

H. jaxarticum M. Pop.

USSR, Kazachstania, S. Granitov s.n. (E).

Pollen is constricted on equatorial regions, and has narrow colpus margins with microperforate tectum. Pollen size 18.4–22.5 × 10.2–11.7 μm.

H. razoumowianum Fisch. & Helm.

USSR, Kazachstania, G. Tscherkasova 6122 (E).

Pollen broad and smooth sculpture colpus margins. Pollen size 20.0–23.4 × 10.9–13.1 μm.

H. songolicum Bongard.

USSR, Kasachstania, 25 June 1959, V. Goloskokov s.n. (E).

Pollen grains broad and smooth marginate colpi and smaller muri. Pollen size 16.6–18.6 × 9.2–11.2 μm.

H. taschkenticum M. Pop.

USSR, Kazachstania, H. Granitov s.n. (E).

Pollen grains operculate colpus membrane and has tectum distinctive proximally bumpy due to protruded columellae. Pollen size 17.9–20.3 × 10.1–12.1 μm.

(5-2-5) Section **Subacaulia** (Boiss.) B. Fedtsch.

H. cephalotes Franchet.

USSR, 4 July 1968, B. Abemuceu et al. s.n. (E).

Pollen grains have more wider lumina and colpus with smooth and broad margins and with granulate membranes in one row. Pollen size 19.8–21.2 × 12.0–14.5 μm.

H. ferganense Korsh.

USSR, Kirghizia, 30 June 1968, B. Saltanova s.n. (E).

Pollen grains have colpus with operculate membranes, and muri thinner in thickness. Pollen size 18.7–22.1 × 10.7–12.1 μm.

H. grandiflorum Pall.

USSR. Orenlury (E).

Pollen size 18.2–20.7 × 10.8–12.2 μm.

H. kumaonense Benth. ex Baker.

Nepal, Tukucha, 29 May 1954, Stainton et al. 803 (TI); Nepal, Chairogaon, Stainton et al. 856 (TI).

H. lehmannianum Bunge.

Asia media, Pamiralaj, 28 July 1930, Pazij and Uironov s.n.

(E).

Pollen grains have very distinctive exine sculpture with supratectal structure, and has well developed colpus membranes. Pollen size 20.2–25.8 × 13.6–16.8 μm.

H. microphyllum Turcz.

Siberia, Turzaninow s.n. (E).

Pollen grains have colpus with smooth and broad margins. Pollen size 18.3–21.4 × 10.0–12.3 μm.

H. monophyllum A. Boriss.

Asia media, Pamiralaj, 28 July 1935, Dshanaera s.n. (E).

Pollen grains have narrow colpus margins with perforate tectum, muri distinctive bumpy. Pollen grains constricted on equatorial regions. Pollen size 19.8–24.0 × 10.9–13.5 μm.

H. poncinsii Franchet.

China, Mts. Tian Shan, 20 June 1930, F. Ludlow 695 (E).

Pollen grains have colpus with smooth and broad margins. Pollen size 18.3–21.5 × 11.3–13.4 μm.

H. splendens Fisch.

Songaria, Chin ad locum Saisang-Nor., Collector unknown (E).

Pollen grains have colpus membrane often not persistent in acetolysed grains. Pollen size 17.7–20.5 × 10.2–11.5 μm.

(5-3) Subgenus **Heteroloma** (Basiner) B. Fedtsch.

H. mongolicum Turcz.

China, Men-Pu 305 (TUS); China, near Hailar, P. H. Dorsett and J. H. Dorsett 3673 (E); Mongolia Occidentalis, 1871, N. M. Przewalski s.n. (E).

Pollen size 15.9–18.8 × 10.3–12.8 μm.

H. multijugum Maxim.

China, Kansu, Parrer and Purdom 668 (TUS); China, Kansu, Umemura 19 (TI); E. Tibet, Ba Valley, J. F. Rock 14363 (E).

Pollen size 15.8–18.2 × 10.4–11.5 μm.

(6) **Onobrychis**

O. oxyodenta Boissier & Huet.

Turkey, Ladik, C. Tobey 734 (TUS).

Pollen size 26.2–30.4 × 12.3–15.5 μm.

O. viciaefolia Scop.

Alpes, Larsen s.n. (TUS).

Pollen is very similar to that of *O. oxyodenta*.

(7) **Stracheya**

S. tibetica Benth.

Nepal, Dolpo, J. B. A. Stainton 4389 (TI); Nepal, Tingjegaon, O. Polunin et al. 1158 (TI).

Pollen size 23.6–27.8 × 14.8–17.8 μm.

(8) **Taverniera**

T. nummularia DC.

Orientale, 1868, Haussknesht s.n. (BM); Perciae, Haussknescht 20061 (BM).

Pollen size 16.9–18.8 × 11.9–13.5 μm.

崔　秉熙，大橋広好: マメ科イワオウギ属およびその近縁属の花粉形態と分類

マメ科イワオウギ属およびその近縁属はイワオウギ連に属す．イワオウギ連は以前は節果をもつマメ亜科の種をまとめたものであつたが，近年は小托葉を欠く羽状複葉を持ち，花は腋生の総状花序につき，龍骨弁は鈍頭で，ふつう多数の胚珠を持ち，節果をつくる群とまとめられている．Hutchinson（1964）はイワオウギ連に9属を含めたが，Polhill（1981）は7属とした．両説の違いの原因は属の範囲と特徴が十分に定められていないためと考えられる．特にこの連の中心であるイワオウギ属が問題となる．イワオウギ属のモノグラフはFedstchenko（1899, 1902）が作り上げたが，その後多くの種が発表され，また，当時の命名法で分類体系が整理されているため，今日では全く不完全なものとなっている．

イワオウギ連では花粉形質の異同が分類体系を構築するための重要な形質であることが明らかにされている（Ohashi 1971, Ferguson and Skvarla 1981）．そこで，本研究ではHutchinsonによってイワオウギ連に分類された属のうち1属を除き，他の8属全て（*Alhagi, Corethrodendron, Ebenus, Eversmannia,* イワオウギ属, *Onobrychis, Stracheya* および *Taverniera*）と特にイワオウギ属では全ての属内分類群にわたり，合計51種を対象として，花粉形態を調べ，分類体系との関連を考察した．

花粉粒は3溝粒3-colpate, 3溝孔粒3-colporate, 類3溝孔粒3-colporoidateの3型がみられた．3溝粒と3溝孔粒とは類3溝孔粒から進化した花粉型であり，イワオウギ連では最も原始的であると推定した．類3溝孔粒はイワオウギ属イワオウギ亜属にのみ見られた．また，*Corethrodendron, Stracheya* および *Taverniera* はイワオウギ属と花粉形態からは区別できないことを明らかにした．

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